MORPHOMETRIC STUDIES OF THE GENUS *TASMANNIA* (WINTERACEAE) IN VICTORIA, AUSTRALIA

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ABSTRACT

Raleigh, R.E., Ladiges, P.Y., Entwisle, T.J. & Drinnan, A.N. Morphometric studies of the genus *Tasmannia* (Winteraceae) in Victoria, Australia. **Muelleria 8(2): 235–256.** — Collections of *Tasmannia xerophila* (P.Parm.) Gray (Alpine Pepper) and *T. lanceolata* (Poir.) A.C.Smith (Mountain Pepper) were made to test the validity of infrageneric taxa of various circumsciptions and rank that have been applied to populations of *Tasmannia* occurring in Victoria. Populations were compared using morphological attributes analysed by phenetic methods, and by examining flavonoid composition. The name *T. vickeriana* (A.C.Smith) A.C.Smith is reinstated for a variant restricted to the Baw Baw Ranges. It is a compact shrub to *c.* 1 m, with leaves less than 2 cm long (rarely to 2.5 cm), burgundy-coloured aggregate fruit, and white aborted ovules. A robust form of *T. xerophila* from Errinundra Plateau reaching 2.5–4.0 m in height, with leaves to 14 cm long and 3 cm wide and generally thinner than those of *T. xerophila s. str.* has been recognised at subspecific rank, as *T. xerophila* subsp. *robusta. Tasmannia lanceolata* differs from all these taxa in having leaves with usually acute apices; flowers with three or more tepals (cf. two in all members of the *T. xerophila* complex); stamen filaments with a distally branched vascular trace between pollen sacs; and solitary, globose berries bearing a distinct stigmatic furrow. The flavonoid compositions of *T. xerophila* subsp. *xerophila, T. xerophila* subsp. *robusta* and *T. vickeriana* are almost identical, with the sole descriminator being a three-fold decrease in one unidentified compound in *T. vickeriana.* Leaf flavonoid composition of *T. lanceolata* was distinct, having only one flavonoid in common with the other taxa studied. *Tasmannia xerophila* and *T. lanceolata* are sympatric in several localities, but no hybrids were detected by morphometric and biochemical analyses, and flowering times of the two taxa do not overlap.

INTRODUCTION

This study was initiated to clarify the circumscription and number of taxa in *Tasmannia* for the forthcoming *Flora of Victoria* treatement of Winteraceae. Using morphological and biochemical data, the status of taxa within *T. xerophila s. lat.* is reassessed and their separation from *T. lanceolata* verified. Flower and fruit structure and development are detailed because of their likely importance in phylogenetic studies of the family.

Historical review

In 1808, Jean L.M. Poiret (in Lamarck 1808) described a new genus *Winterana* (as '*Winterania*'), including the species *W. lanceolata* which was based on a Labillardière collection from 'côtes de la Nouvelle-Hollande'. This was the beginning of considerable nomenclatural confusion (Table 1). The same taxon was named *Tasmannia aromatica* by de Candolle in 1818 (from a manuscript name of Robert Brown), and then transferred to *Drimys* (as *D. aromatica*) by Mueller (1862) with a description so broad that it easily encompasses the two taxa presently known as *T. lanceolata* (Poir.) A.C.Smith and *T. xerophila* (P. Parm.) M.Gray. Baillion (1868) resurrected the valid epithet '*lanceolata*', renaming the

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Table 1. History of nomenclatural changes for Victorian species of *Tasmannia*

Publication	*T. lanceolata*	*T. xerophila*	*T. vickeriana*
Poiret 1808	*Winterania lanceolata* Poir.	—	—
de Candolle 1818	*Tasmannia aromatica* R.Br. *ex* DC.	—	—
F. Mueller 1862	*Drimys aromatica* (R.Br. *ex* DC.) F. Muell.	*D. aromatica*	—
Baillion 1868	*D. lanceolata* (Poir.) Baill.	—	—
P. Parmentier 1896 (as *in sched.*)	*D. xerophila* [*aromatica*] var. *aromatica* P. Parm.	*D. aromatica*	*D. xerophila* [*aromatica*] var. *alpina* F. Muell. *ex* P. Parm.
Vickery 1937	*D. lanceolata*	*D. lanceolata*	*D. lanceolata* var. *parvifolia* Vickery
Smith 1943	*D. lanceolata*	*D. lanceolata*	*D. vickeriana* A.C. Smith
Willis 1957	*D. lanceolata*	*D. xerophila*	*D. xerophila*
Smith 1969	*T. lanceolata* (Poir.) A.C. Smith	*T. lanceolata*	*T. vickeriana* (A.C. Smith) A.C. Smith
Vink 1970	*D. lanceolata*	*D. piperita* entity 39 '*xerophila*'	*D. piperita* entity 39 '*xerophila*'
Willis 1972	*D. lanceolata*	*D. xerophila*	*D. xerophila*
Gray 1976	[*T. lanceolata*]	*T. xerophila* (P. Parm.) M. Gray	*T. xerophila*
Ross 1990	*T. lanceolata*	*T. xerophila* *T.* sp. (Errinundra Plateau)	*T. xerophila*

taxon *D. lanceolata* (Poir.) Baill. Until 1896, only one taxon was recognized from Victoria.

In an ambiguous paper, Parmentier (1896) delineated *D. aromatica, D. xerophila* P.Parm., and two varieties, var. *β aromatica* P.Parm. and var. *alpina* F.Muell. *ex* P.Parm., all occurring in Victoria. In what seems a perplexing error, the variety names were published under *D. aromatica*, although it seemed to be Parmentier's intention to rank the two varieties under his new species *D. xerophila. Drimys xerophila* var. *alpina* was described briefly as a small-leaved plant growing in the Baw Baw Ranges, but its type incorrectly cited (Parmentier 1896, p. 226) as from Mt Bischoff in Tasmania (see Willis 1957 and Vink 1970).

Since the early 1900s only two taxa have been recognised for Victoria, but under various names and circumscriptions. In 1937, *D. aromatica* (synonymous with Parmentier's *D. xerophila* var. *β aromatica*) was renamed *D. lanceolata* and *D. xerophila* considered a synonym (Vickery 1937, Smith 1943). The small-leaved *D. xerophila* var. *alpina* was renamed *D. lanceolata* var. *parvifolia* in 1937 by Vickery and then elevated to specific rank as *D. vickeriana* by Smith (1943). Willis (1957) declared *D. lanceolata* and *D. xerophila* 'good' taxa but judged the small-leaved *D. vickeriana* to be synonymous with *D. xerophila*. Willis noted it as an 'unusually small-leaved, small-flowered state of *D. xerophila*', and considered it merely a polymorphism induced by environmental factors. *Tasmannia* was reinstated by Smith (1969) who maintained two taxa, *T. vickeriana* and *T. lanceolata*. However, Vink (1970) retained the generic name *Drimys*, referring *D. xerophila* to one of many 'entities' in the highly polymorphic *D. piperita* (with *D. vickeriana* as a synonym). Willis (1972) maintained his 1957 nomenclature, but in 1976, *Drimys xerophila* was transferred to *Tasmannia* by Gray. In the third edition of *A Census of the Vascular Plants of Victoria* (Ross 1990), three taxa are listed: *T. lanceolata*, *T. xerophila* and *T.* sp. (Errinundra Plateau), the latter an un-named taxon based on a population at Goonmirk Rocks. The designations used in the fourth edition of the *Census* (Ross 1993) follow the conclusions of the current study.

MATERIALS AND METHODS

Sites and sampling

Three main collection sites were located at Mt Baw Baw and in the Mt Buffalo and Errinundra Plateau National Parks, Victoria. Three localities in Errinundra National Park were sampled, viz. Frosty Hollow, Goonmirk Rocks and Mt Ellery; *Tasmannia lanceolata* and *T. xerophila* are sympatric at the latter two areas (Fig. 1). Five male and five female plants were sampled at each locality. Single collections were made from a range of other sites including Mt Kosciusko, Brindabella Range, Mt Selwyn (NSW), the Grampians and Otway Range. Flowering material of *T. xerophila s. lat.* was collected between December 1991 and January 1992, and of *T. lanceolata* during September 1992. Fruiting material from all taxa was collected between April 1992 and June 1992. Collection details are included with the taxonomic summary. Voucher specimens were lodged at The University of Melbourne Herbarium (MELU) with duplicates at the National Herbarium of Victoria (MEL).

Leaves, flowers and fruit from all taxa were preserved in either FAA (Formalin: glacial acetic acid: 85% ethanol in the proportions 2:1:17) or in MAA (as for FAA but substituting Mirsky's fixative (National Diagnostics) for formalin). Leaves and fruit were collected and dried in paper bags in a drying cabinet. Fresh material was stored at 4°C until examined. Twenty leaves (up to 50 for the small-leaved *Tasmannia*) were removed from each of 10 plants sampled at each site and dried in paper bags for analysis of leaf flavonoids.

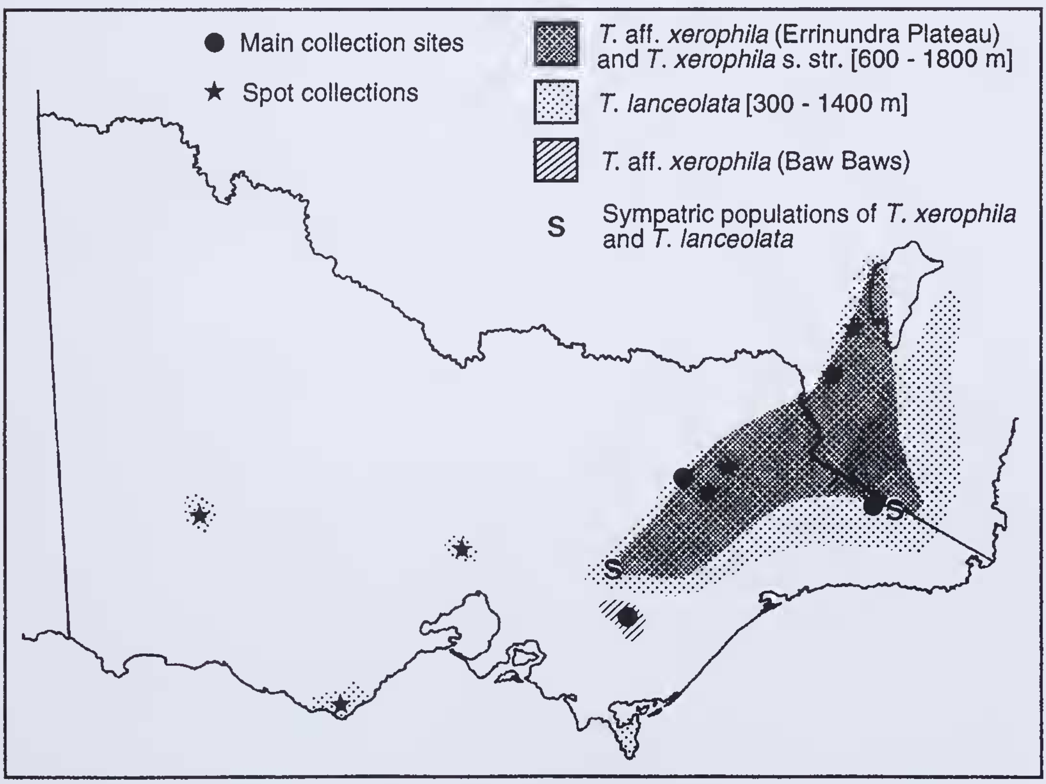

Fig. 1. Geographic distribution of *Tasmannia* in Victoria and south-eastern New South Wales.

Approximately 300 specimens from herbaria were examined, including type specimens from the Muséum National d'Histoire Naturelle (P), *T. xerophila* from the National Herbarium of New South Wales (NSW) and all Victorian *Tasmannia* held at MEL.

Microscopy

Leaf fragments, flowers, stamens and carpels examined by scanning electron microscopy were first critical point dried and sputter-coated with gold. Pollen for scanning electron microscopy was air dried. Carpels examined by light microscopy were embedded in London Resin, sectioned at 4 µm on a glass knife and stained with Toludine Blue. Whole flowers were cleared in a solution of 1% Basic Fuchsin in 10% NaOH at 60°C following the procedure of Fuchs (1963).

Morphological measurements

Measurements were analysed from a total of 84 plants for which 10 mature leaves, 10 inflorescences, 10 flowers and 10 fruiting pedicels were available. Dried leaves were re-hydrated by soaking in hot water for 30 min. Twenty-six morphological characters were scored: 4 qualitative and 22 quantitative (Table 2). The score for each quantitative character was the mean of 10 measurements. Linear measurements and derived ratios describing shape were included in the data set. Some controversy has been associated with using ratios as characters; however, since it was not known *a priori* whether taxa would differ in size or shape or a combination of both, the use of ratio as shape characters was considered justifiable and appropriate (Hills 1978).

Data were analysed phenetically using the PATN computer package (Belbin 1987). Quantitative data were range-standardised and qualitative data were unstandardised. The Manhattan metric (Williams 1976) association measure was

Table 2. Characters included in analyses

Quantitative characters
1. Leaf length (L mm)
2. Leaf width (W mm)
3. Distance to widest point of leaf (DWP mm)
4. Petiole length (LP mm)
5. L/W
6. L/DWP
7. L/LP
8. Fruit diameter (FD mm)
9. Fruit pedicel length (FPL mm)
10. Stigmatic furrow length (LSC mm)
11. Flower pedicel length (PL mm)
12. Fruit per pedicel (FP)
13. Fruit scars per pedicel (FSP)
14. Carpels per flower (CNo.)
15. Ovules per carpel (ONo.)
16. Aborted ovules per fruit (ANo.)
17. Seed per fruit (SNo.)
18. SNo./ONo.
19. Flowers per inflorescence (FNo.)
20. Tepals per flower (PNo.)
21. Stamens per flower (STNo.)
22. Sterile carpels per male flower (SCF)
Qualitative characters
23. Ovule colour (OC): pink (1), not pink (0)
24. Fruit colour:
Black (FCBl/0.33), not black (0)
Burgundy-grey (FCBg/0.33), not burgundy-grey (0)
Burgundy-red (FCBr/0.33), not burgundy-red (0)
25. Fruit groove (FT): indistinct (1), distinct (0)
26. Tubercles on stem (STEM): present (1), absent (0).

used to calculate a dissimilarity matrix and individual plants were clustered using both Unweighted Pair-Group Method using arithmetic Averages (UPGMA) and Weighted Pair-Group Method using arithmetic Averages (WPGMA). Cramer values were calculated to determine which characters best discriminated the final groups identified. The dissimilarity matrix was also used for ordination by Hybrid Multi-Dimensional Scaling (HMDS; Faith *et al.* 1987). Since multi-dimensional scaling is sensitive to locally minimal solutions depending upon the starting point used (Kruskal 1964a, 1964b), 20 ordination analyses were performed using different random starting configurations. Each ordination was similar and the result with the lowest stress value (i.e. with the 'best fit') is presented.

A second matrix, a subset of 53 individuals and 22 quantitative characters that excluded populations of small-leaved *Tasmannia* and *T. lanceolata*, was analysed in the same way. This matrix was restandardised by range because extreme values were different. Those characters that were constant for all individuals were removed.

Flavonoid chromatography

Leaves were dried for at least 4 days, then ground to a fine powder. Samples of 1–6 g were placed in air-tight 30 ml glass vials with 80% aqueous methanol submerging the material by 10 mm. After 24 hours the supernatant was decanted and leaf extracts applied to sheets of Whatman 3MM (46 × 57 cm) chromatography paper and run in two dimensions (Mabry *et al.* 1970). The first run (for 36 hours) used tertiary butyl alcohol (TBA) and the second run used acetic acid (for 12–24 hours). Dry chromatograms were viewed in normal light and under UV light (336 nm) in the presence of ammonia vapour, and all spots noted. Spots on different sheets were considered to represent the same compound if they exhibited the same colours under both viewing conditions and their positions on the paper were the same. No attempt was made to chemically characterize any compound.

RESULTS

To simplify comprehension, the names accepted as a result of this study are used throughout the remainder of the paper: i.e. *T. xerophila* subsp. *robusta* for '*T. xerophila*' from the Errinundra Plateau, *T. vickeriana* for '*T. xerophila*' from the Baw Baws, *T. xerophila* var. *xerophila* for the remaining plants referable to *T. xerophila*, and *T. xerophila s. lat.* for all plants previously included within *T. xerophila.*

Distribution, habitat & habit

Tasmannia lanceolata is widespread, extending from Tasmania, through Victoria to New South Wales and Australian Capital Territory (Fig. 1). It grows as a shrub to small tree (1.5–4.0 m) at altitudes of between 300–1400 m in sites of high annual rainfall (mostly > 1000 mm). In several localities (e.g. Lake Mountain and Goonmirk Rocks), *T. lanceolata* is sympatric with *T. xerophila s. lat.* but it grows generally in wetter soils and at lower altitudes. Habitats range from dry open-forest to wet tall open-forest and rainforest. *Tasmannia lanceolata* is usually single-stemmed, although plants in disturbed areas may have 4–5 stems. Young branchlets are red and tubercules are absent. At Mt Ellery, Goonmirk Rocks and in the Grampians, *T. lanceolata* grows among granite outcrops, and at other sites is often found along watercourses.

Tasmannia xerophila s. lat. occurs throughout the central highlands of Victoria, mostly as a common understorey shrub (0.6–2 m) in subalpine *Eucalyptus pauciflora s. lat.* woodland at altitudes between 600 and 1800 m. Its range extends into New South Wales and the western edge of Australian Capital Territory. A robust form of *T. xerophila, T. xerophila* subsp. *robusta,* is found at high rainfall sites (mostly >1500 mm) in East Gippsland (e.g. Goonmirk Rocks and Mt Ellery) where plants grow to 4 m in height. At these sites this robust form is sympatric with *T. lanceolata*, and it has been suggested that it may be of hybrid origin. Small-leaved *Tasmannia*, *T. vickeriana*, has the most restricted distribution of all Victorian species of *Tasmannia* and is only found in the Baw Baw Ranges, where it grows as a small shrub (0.6–1.2 m) under *E. pauciflora s. lat.*

Although *Tasmannia xerophila* subsp. *xerophila* grows generally in subalpine *Eucalyptus pauciflora* woodland, it also occurs in open-forest and as isolated plants in subalpine grasslands. Plants often grow amongst granite boulders or along watercourses. Individual plants are clumped as a result of root suckering near the base of each plant. The only seedlings found were growing in *Sphagnum* along a water channel near Falls Creek. Most plants have many stems, with up to 30 stems counted in one area, possibly indicating considerable age. Stems are finely tuberculate and ochre to brown in colour; young branchlets are red. At Mt Buffalo in the area around 'The Horn', which was burnt between 1986–1987, plants of *T. xerophila* subsp. *xerophila* are only *c.* 0.8 m in height but have numerous stems, suggesting regeneration from rootstock rather than from seed.

Tasmannia xerophila subsp. *robusta* grows in wet tall open forest and at slightly lower altitude than *T. xerophila* subsp. *xerophila* At Goonmirk Rocks, it grows 2–4 m in height and forms multistemmed, clumped individuals amongst *Podocarpus lawrencei* Hook. f.

Tasmannia vickeriana occupies a similar habitat to *T. xerophila* subsp. *xerophila* at altitudes between 1300–1500 m in *Eucalyptus pauciflora* woodland. It forms clumped individuals up to 1.5 m across but rarely more than 1.2 m in height, and has a more compact habit than *T. xerophila* subsp. *xerophila.* Stems are finely tuberculate and young branchlets are red. Mature stems are ochre to brown. No juvenile plants were found.

Leaf morphology and anatomy

Leaves of most *T. xerophila s. lat.* range in length between 3–9 cm, but are up to 14 cm in *T. xerophila* subsp. *robusta* and as short as 0.8 cm in *T. vickeriana.* Leaves are coriaceous, usually with obtuse apices and between 2–30 mm wide. The adaxial surface of the leaf is dark green, the abaxial surface paler and glaucous. Veins of the leaf are usually obscured in *T. xerophila* subsp. *xerophila* but more obvious in *T. xerophila* subsp. *robusta.* The leaves of these two taxa are *c.* 450 μm thick and the epidermis consists of a single row of cells (Fig. 2a). Leaf anatomy of *T. vickeriana* (Fig. 2b) is similar to that of *T. xerophila* subsp. *xerophila* and *T. xerophila* subsp. *robusta* but leaves are thicker (*c.* 540 μm), as is the cuticle. Leaves of *T. vickeriana* are coriaceous and seldom exceed 2 cm in length (some leaves on a bush may reach 2.5 cm) and 6 mm in width.

Leaves of *T. lanceolata* range in length from 4–12 cm with usually acute apices. However, a few herbarium specimens collected from areas such as

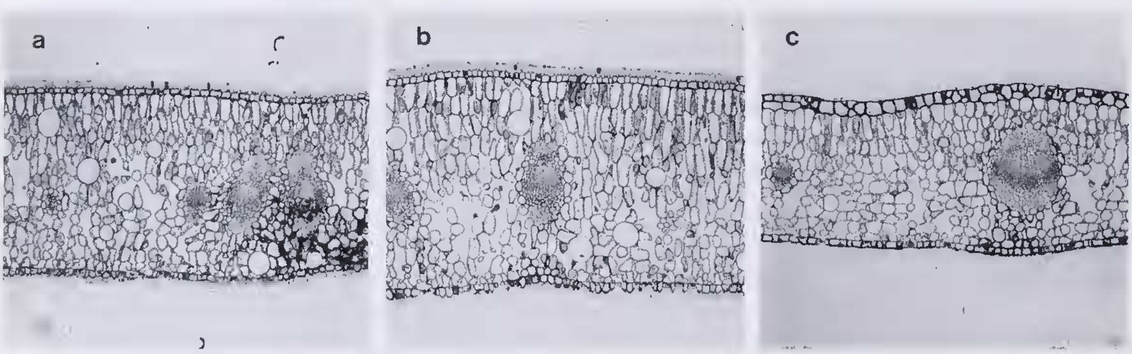

Fig. 2. Leaf sections (light micrographs) ×70. a — *T. xerophila* subsp. *xerophila.* b — *T. vickeriana.* c — *T. lanceolata.*

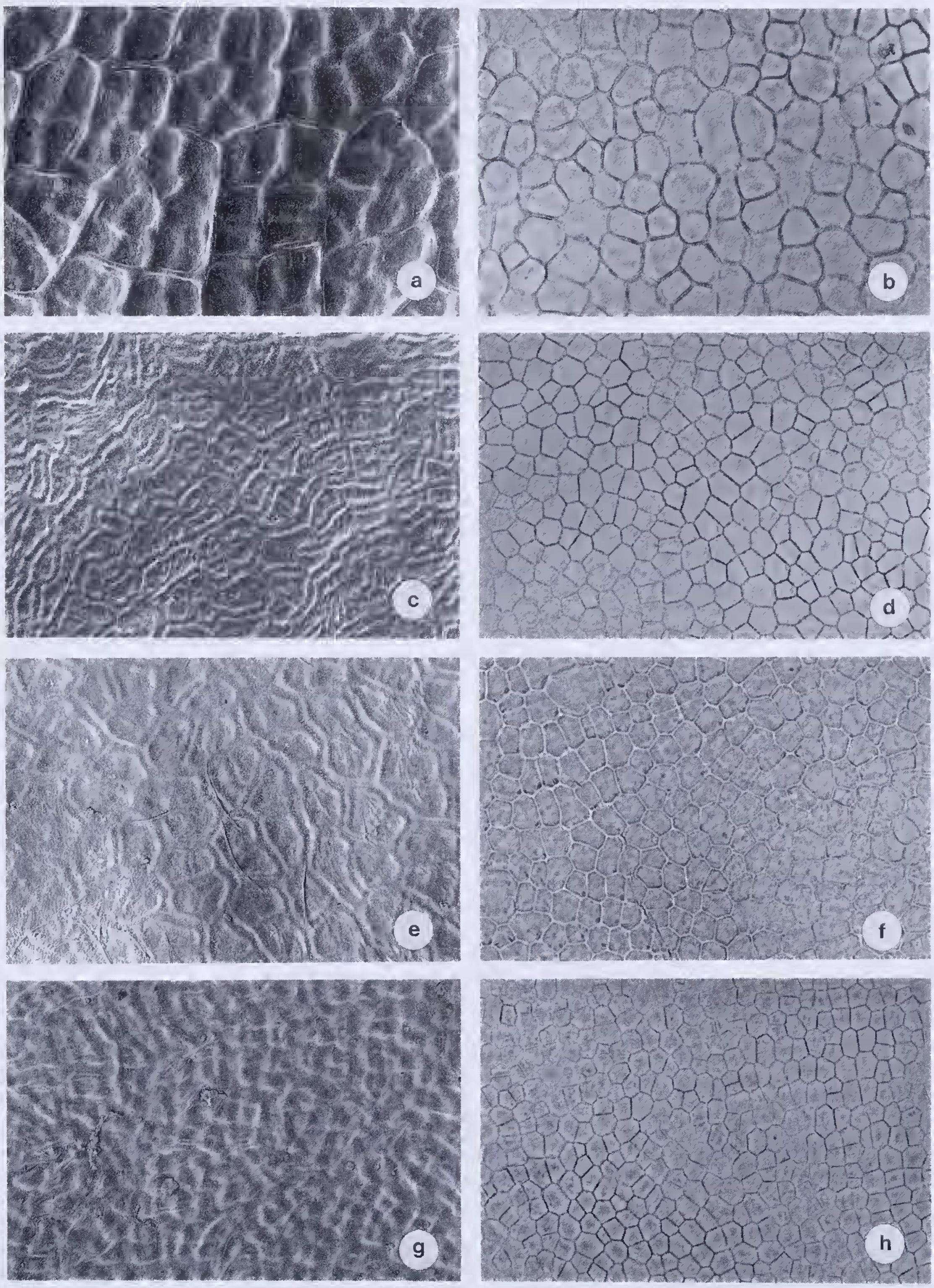

Fig. 3. Leaf upper surfaces and epidermal cells ×200 (a,c,e,g — scanning electron micrographs; b,d,f,h — light micrographs). a,b — *T. lanceolata*. c,d — *T. xerophila* subsp. *xerophila* e,f — *T. xerophila* subsp. *robusta*. g,h — *T. vickeriana*.

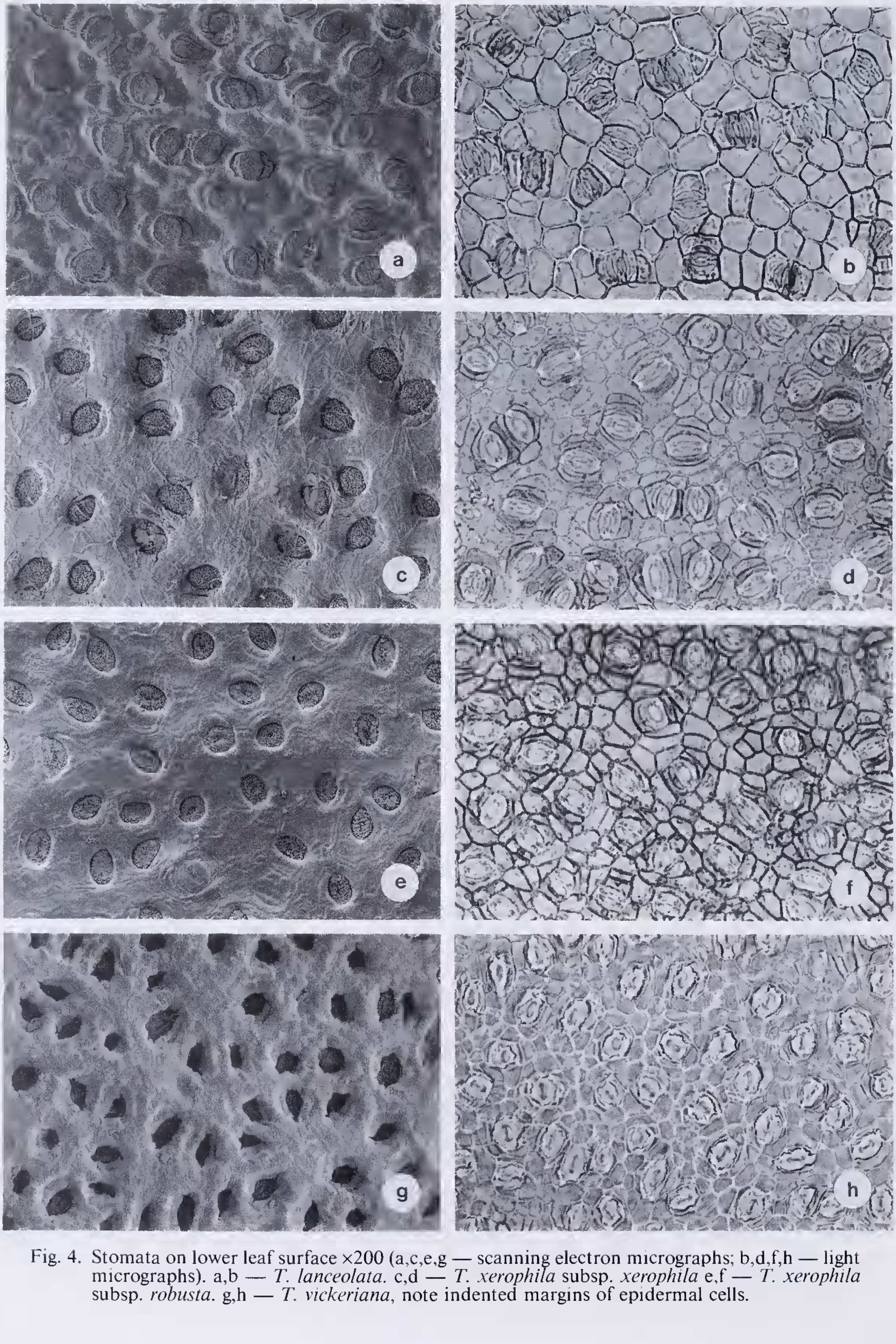

Fig. 4. Stomata on lower leaf surface ×200 (a,c,e,g — scanning electron micrographs; b,d,f,h — light micrographs). a,b — *T. lanceolata*. c,d — *T. xerophila* subsp. *xerophila* e,f — *T. xerophila* subsp. *robusta*. g,h — *T. vickeriana*, note indented margins of epidermal cells.

Mt Field and Mt Wellington in Tasmania and referred to *T. lanceolata* (based on fruit characteristics) have stout, thick leaves with obtuse apices. The adaxial surface of the leaf of *T. lanceolata* is paler than that of *T. xerophila s. lat.* but similarly glaucous on the abaxial surface. Veins of the leaf are prominent. Leaf width is 8–35 mm and leaves are thinner (*c.* 340 µm) than those of *T. xerophila s. lat.* Leaves of *T. lanceolata* have thin cuticles (Fig. 2c) and the epidermis of the adaxial surface is characterised by multiple layers of cells. All taxa had well-defined palisade and spongy mesophyll confirming the findings of Sampson *et al.* (1988), but contrary to Willis (1957) who reported a well defined palisade layer only in *T. lanceolata.*

Leaves examined by scanning electron microscopy revealed different epidermal cell shapes and sizes between taxa (Figs 3a,c,e,g). The patterns are similar in *T. xerophila* subsp. *xerophila* and *T. xerophila* subsp. *robusta*, but upper leaf surfaces of *T. vickeriana* are more similar to those of *T. lanceolata*, although with much smaller cells. Adaxial epidermal cells of *T. lanceolata* (Fig. 3b) are about twice the size of epidermal cells of *T. xerophila s. lat.* (Figs 3d,f,h), but there is no obvious variation within the latter.

Stomata are always found on the abaxial leaf surface in *Tasmannia* and are heavily occluded by waxy material in all variants of *T. xerophila s. l.* (Figs 4c,e,g). Stomata of *T. lanceolata* are either completely clear or only lightly occluded by waxy material (Fig. 4a). Guard cells of *T. lanceolata* are prominent (Fig. 4a) but those of *T. xerophila* subsp. *xerophila* and *T. xerophila* subsp. *robusta* are usually obscured by a thicker cuticle (Figs 4c,e), the guard cells of *T. vickeriana* being totally hidden by a very thick cuticle (Fig. 4g). Stomata in the *T. vickeriana* are overhung by epidermal cells with indented margins (Fig. 4h). Stomatal density is similar in all forms of *T. xerophila* (Fig. 4d,f,h) but lower in *T. lanceolata* (Fig. 4b).

Floral morphology and phenology

Flowers of *T. xerophila s. lat.* are arranged in a pseudo-terminal inflorescence below a dormant vegetative bud. Pistillate flowers are white in bud and arise from the axil of a bract. The outer bracts of the immature inflorescence are largest and continue to enclose flower buds as they develop. The prophylls (calyx) recurve backwards after flowers have opened. Pistillate flowers have two creamy, strap-shaped tepals (sometimes with a greenish tinge) inserted alternate to the prophylls (Fig. 5a). When there are three tepals, the third tepal is often intermediate between a tepal and a carpel, in the position of a carpel. In *T. xerophila* subsp. *xerophila* and *T. xerophila* subsp. *robusta*, the number of carpels per flower varies from 2–11 (most often 3–6), while in *T. vickeriana*, carpels vary from 1–6 per flower (most often 1 or 2). Carpels are D-shaped and the stigmatic crest is positioned along the apex of the carpel along the distal portion of the ventral suture (Figs 5b,c). In *T. xerophila* subsp. *xerophila* and *T. xerophila* subsp. *robusta*, carpels contain 2–9 ovules arranged in two rows along the ventral line; carpels of *T. vickeriana* contain 3–6 ovules similarly arranged. All populations of *Tasmannia xerophila* flower between early December and early February when *T. lanceolata* is already in fruit.

Tasmannia lanceolata commences flowering in late September and finishes in late November. Each flower arises from the axil of a bract and is arranged in a more compact inflorescence than those of the other taxa. The outer bracts of the inflorescence are smaller than the inner bracts and all bracts fall from the inflorescence as buds mature. All observed buds had pinkish prophylls that recurve backwards once flowers opened. Tepals are strap-shaped, cream with a greenish tinge and number between three and nine per flower, usually four or five. Tepals are inserted laterally to the median line of the flower (the median line being the plane along which the prophylls fuse). Pistillate flowers have one globose carpel (occasionally two fused together) containing 9–18 ovules. The stigmatic crest is sunken into a distinct furrow along the ventral suture of the carpel. A flange of

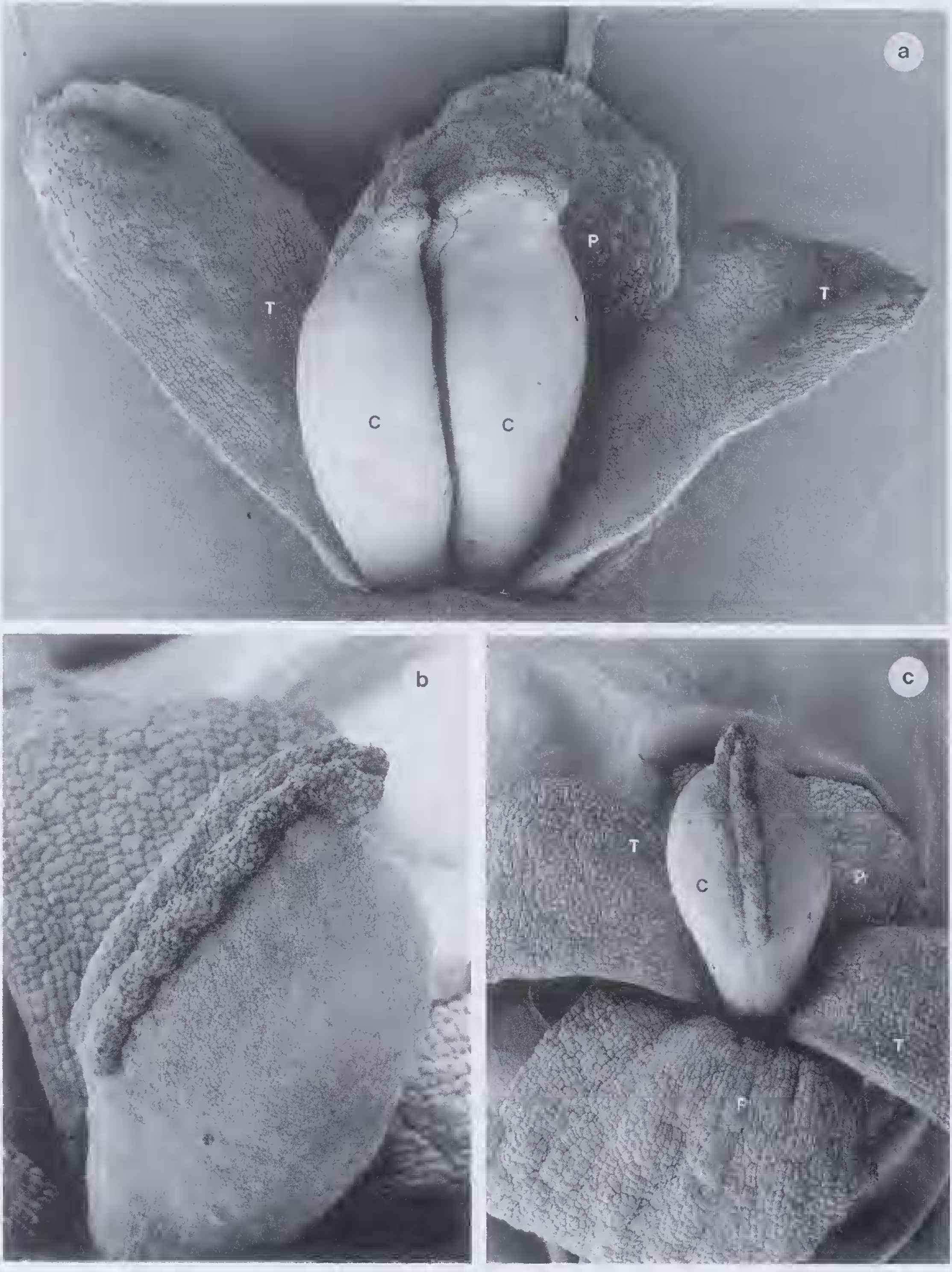

Fig. 5. Pistillate flowers and carpels of *T. xerophila* (scanning electron micrographs); C = carpel, T = tepal, P = prophyll. a — *T. xerophila* subsp. *xerophila* ×35. b — *T. xerophila* subsp. *xerophila* ×50, showing carpel with papillate stigmatic crest. c — *T. vickeriana* ×30.

tissue similar to that seen at the base of single carpels of *T. vickeriana* is located at the base of the carpel. An exudate was observed on the stigma of pistillate flowers of plants grown from cuttings.

In both *T. xerophila s. lat.* and *T. lanceolata*, buds of staminate flowers are larger than pistillate flowers. Each staminate flower has a single sterile carpel at the centre (Figs 6a,b). In *T. lanceolata*, sometimes two sterile carpels are present and occasionally none. The sterile carpels of all forms of *T. xerophila s. lat.* are similar in morphology, and smaller than the fertile carpels of corresponding pistillate flowers. The sterile carpel in flowers of *T. lanceolata* are more globose than D-shaped (Fig. 6c) and are also smaller than carpels of pistillate flowers. Pollen was observed adhering to the stigmatic crest of staminate flowers of *T. vickeriana*

Fig. 6. Staminate flowers (a,b,c — scanning electron micrographs; c — light micrograph); C = carpel, T = tepal, P = prophyll. a — *T. vickeriana* ×12, note sterile carpel. b — *T. vickeriana* ×70, note pollen adhering to stigmatic crest of the sterile carpel. c — *T. lanceolata*, ×50, note sterile carpel with stigmatic crest overtopping the carpel. d — *T. xerophila* subsp. *xerophila* ×100, section through sterile carpel (ovules are absent).

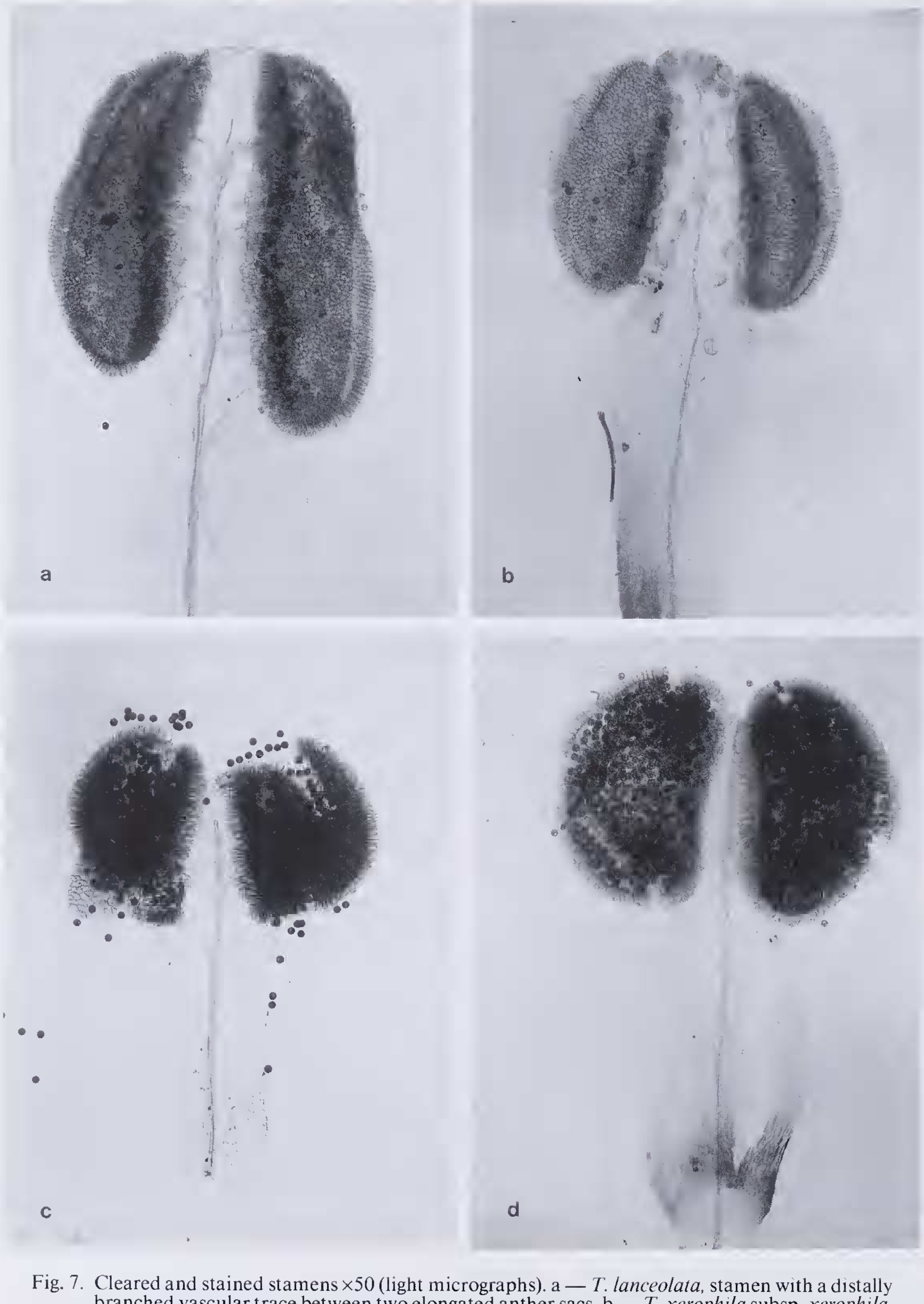

Fig. 7. Cleared and stained stamens ×50 (light micrographs). a — *T. lanceolata*, stamen with a distally branched vascular trace between two elongated anther sacs. b — *T. xerophila* subsp. *xerophila*, dehisced stamen with an unbranched vascular trace between two anther sacs (darkly staining cells are oil bodies). c — *T. xerophila* subsp. *robusta*, stamen with an unbranched vascular trace. Thickened cells of the anther wall are clearly visible (darkly staining spots are pollen). d — *T. vickeriana*, stamen with an unbranched vascular trace and anther cell walls clearly visible.

(Fig. 6b). Closer inspection revealed the presence of exudate, with the majority of pollen germinated and pollen tubes growing through the stigmatic surface. These sterile carpels lack ovules (Fig. 6d). The number of stamens per staminate flower varies from 7–30 in *T. xerophila s. lat.* and from 18–27 in *T. lanceolata*.

Populations of *T. xerophila s. lat.* all have the same stamen structure. However, a significant difference was noted between stamens of these taxa and those of *T. lanceolata*. The single vascular trace is branched distally between the anther sacs in *T. lanceolata* (Fig. 7a) but unbranched in the other taxa (Figs 7b–d). *Tasmannia glaucifolia* is the only other Australian species reported with an unbranched vascular trace (Sampson *et al.* 1988). Anther sacs are also more elongate. Cells of the anther wall in all taxa are thickened by bands of a lignin-like substance that stains with Basic Fuchsin (like xylem and pollen) when anthers are cleared. Pollen consists of four grains, with a reticulate exine, arranged tetrahedrally in permanent meiotic tetrads and is similar in all taxa. Fiser & Walker (1967) came to the same conclusion after a much broader and more detailed study of *Tasmannia* pollen.

FRUIT AND SEED MORPHOLOGY

Tasmannia xerophila subsp. *xerophila* and *T. xerophila* subsp. *robusta* both have an aggregate fruit with 1–11 berries per pedicel. Berries are green when immature and black at maturity. The stigmatic crest is positioned sub-apically (Fig. 8a). Pedicels with single berries usually have scars where additional berries were attached or where carpels failed to develop. Three berries per pedicel is most common in both taxa. Berries range in length from 6.5–11 mm. Up to seven seeds per berry are found with an ovule to seed conversion ratio of between 45–90%; aborted ovules are pink.

The fruit of *T. vickeriana* is very like that of other members of *T. xerophila s. lat.*, with a similar berry shape and stigmatic crest; however, its colour is burgundy rather than black when mature, and the number of berries per pedicel is 1–4 (most commonly 1 or 2). Up to five seeds per berry are set in *T. vickeriana* with an ovule to seed conversion ratio of 60–86%; aborted ovules are white.

Fruit of *T. lanceolata* is black at maturity, although immature berries are reddish to dark maroon. Each pedicel bears one globose berry (occasionally two)

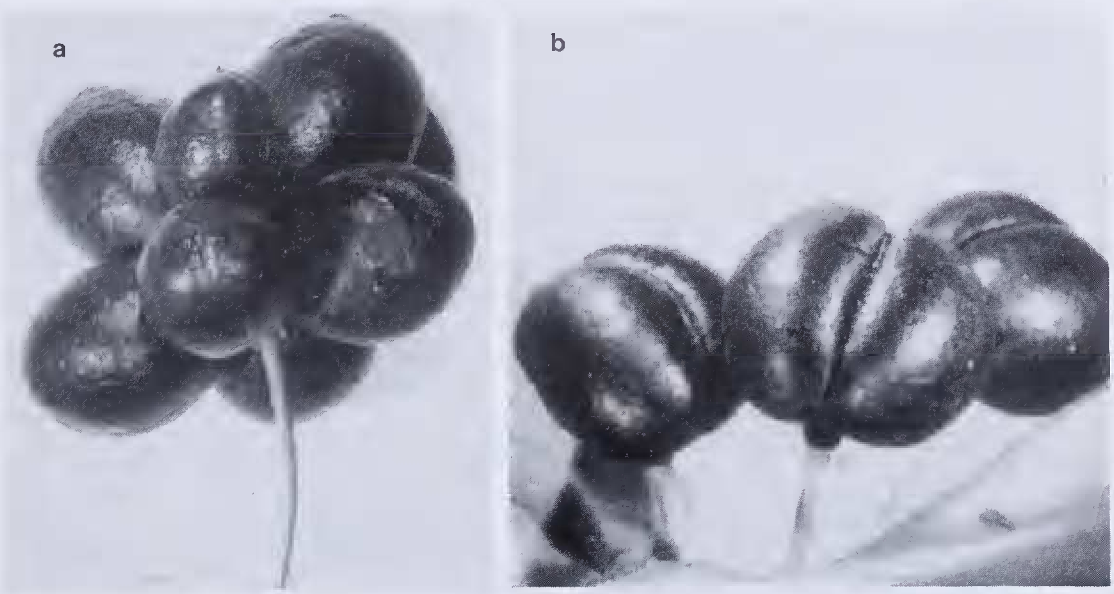

Fig. 8. Mature fruit ×3 (light micrographs). a — *T. xerophila* subsp. *xerophila*, aggregate fruit consisting of sub-ovoid berries with sub-apical stigmatic crest. b — *T. lanceolata*, singular, globose berries with distinct furrow and sunken stigmatic crest.

marked with a distinct furrow along the median line (Fig. 8b). The stigmatic crest is sunken into this furrow and reaches nearly to the base of each berry. Berries are 5.5–7.0 mm in diameter. Up to 13 seeds per berry are set in *T. lanceolata* with an ovule to seed conversion ratio from 23–88%.

The seeds of all taxa are shiny black with a smooth outer surface. Seed of *T. lanceolata* are large and irregular in shape, unlike the rounded seed of *T. xerophila s. lat.*; the seed of *T. vickeriana* is slightly smaller and more rounded than that of other members of *T. xerophila s. lat.* Attempts to grow all four taxa from seed were unsuccessful.

Morphometric analyses

UPGMA clustering of 84 plants was truncated at the 4-group level (Fig. 9). Group 1 consists of 41 plants of *T. xerophila* subsp. *xerophila* from six localities; Group 2 of 13 plants of *T. xerophila* subsp. *robusta* from Mt Ellery and Goonmirk Rocks; Group 3 of 17 plants of *T. vickeriana* from Mt Baw Baw; and Group 4 of 14 plants of *T. lanceolata* from five localities. Groups from WPGMA (Fig. 10) are similar to those from UPGMA, with some differences in the hierarchical clustering. Group 3 and Group 4 are in reverse positions, and three plants from the UPGMA Group 2 are placed in WPGMA Group 1 (Fig. 10).

The ordination of principal axes 1 and 2 (Fig. 11) confirms the pattern from the UPGMA cluster analyses. Within *T. xerophila*, three mostly non-overlapping clusters (groups 1–3) are evident, and clearly isolated from these is *T. lanceolata* (group 4).

Flavonoid compounds

Ten flavonoid compounds were detected, of which only the most abundant one was shared between all taxa (Table 3). As in the morphological analyses,

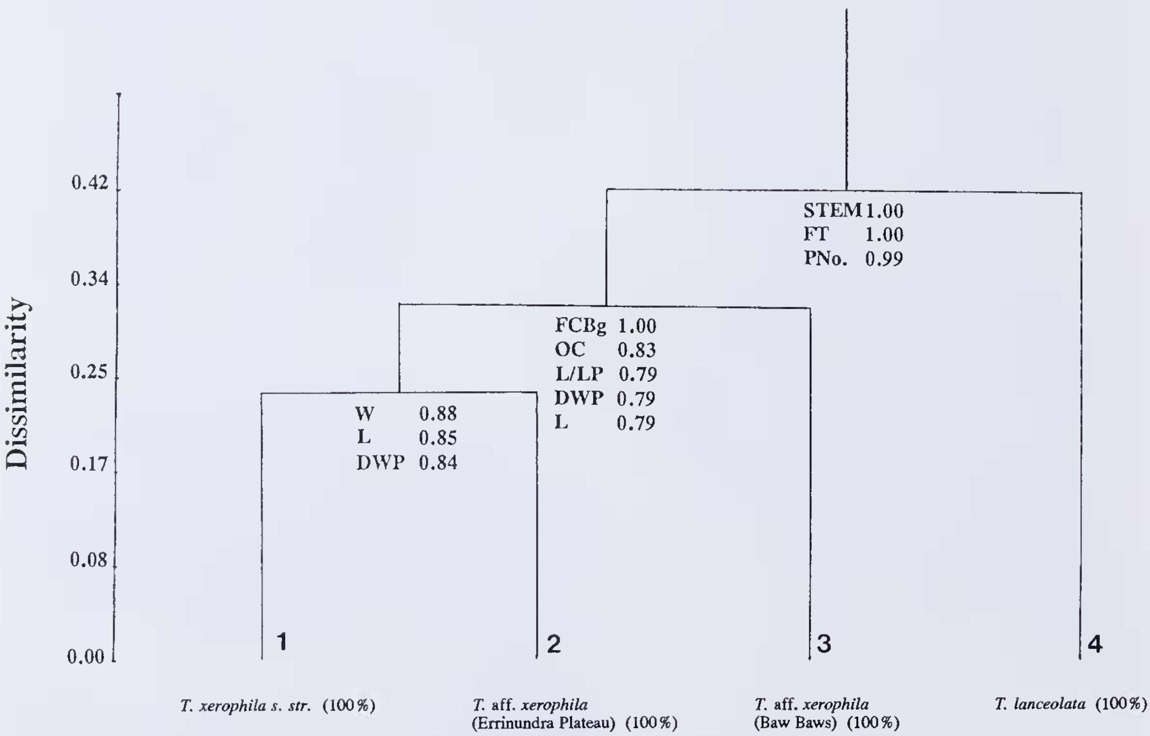

Fig. 9. Dendrogram of individuals of *Tasmannia* based on UPGMA, truncated at the four-group level. Percentages of individuals of each form are given in parentheses and nodes are labelled with characters that correlate most highly with the dichotomy. For abbreviations see Table 2.

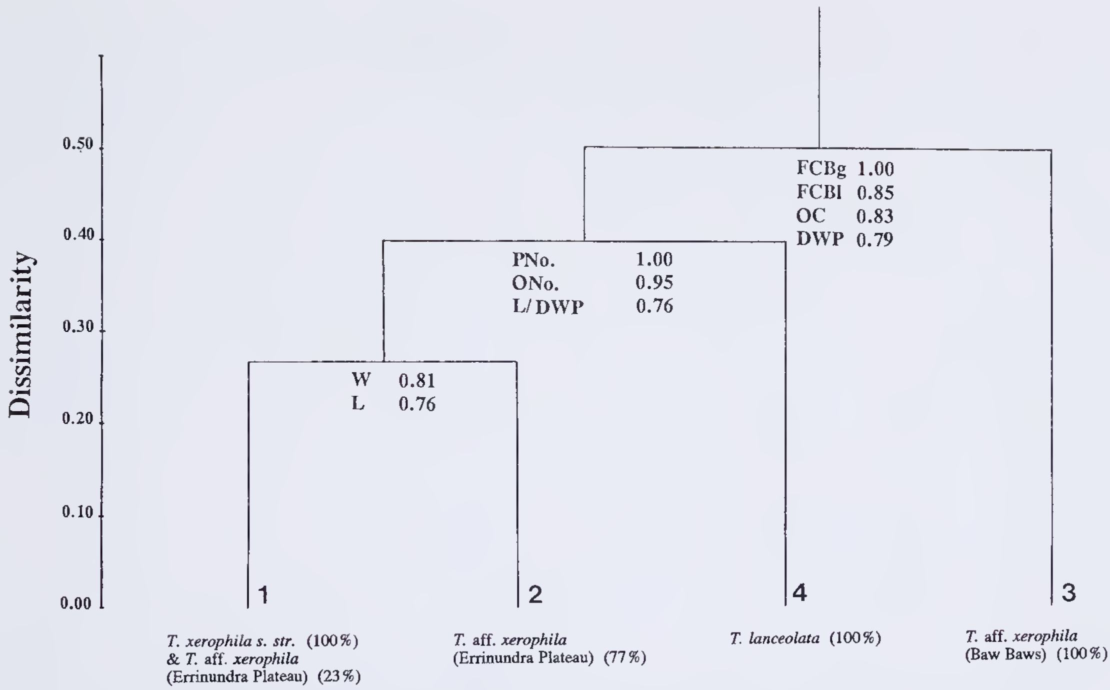

Fig. 10. Dendrogram of individuals of *Tasmannia* based on WPGMA, truncated at the four-group level. Percentages of individuals of each form are given in parentheses and nodes are labelled with characters that correlate most highly with the dichotomy. For abbreviations see Table 2.

T. lanceolata was distinct from *T. xerophila s. lat.* Three compounds were unique to *T. lanceolata* and one was otherwise only found in one plant of *T. xerophila* subsp. *robusta*. The flavonoid profile of *T. lanceolata* was uniform, with no differences between individuals from four populations.

All variants of *Tasmannia xerophila s. lat.* possessed four compounds which were not found in *T. lanceolata*. One compound was found in only a single plant of *T. xerophila* subsp. *xerophila* from Falls Creek. The only difference in flavonoid profiles was quantitative in that *T. vickeriana* consistently showed three-fold less of one compound (indicated by a spot three-fold smaller in diameter than the same spot in other taxa and no change in diameter of other spots on the chromatogram).

DISCUSSION

Classification and ordination analyses demonstrated that the pattern of variation based on morphology includes a number of discrete groups and not a continuum of variation. *Tasmannia lanceolata* is clearly distinct from other taxa in leaf anatomy (having a multi-layered epidermis), stamen venation (branched vascular trace), berry morphology and colour, leaf thickness and shape, and number of tepals.

Within *T. xerophila s. lat.*, *T. vickeriana* is the least variable on morphological characters and forms a relatively uniform cluster with all analyses. It is similar to *T. xerophila* subsp. *xerophila* and *T. xerophila* subsp. *robusta* in floral and berry morphology but different in having burgundy-coloured fruit with white aborted ovules, lower carpel number and ovule number, and consistently smaller leaves. Plants from the Lake Mountain and Mt Buller areas may approach *T. vickeriana* in leaf size but fall within the range expressed by the more variable *T.* aff. *xero-*

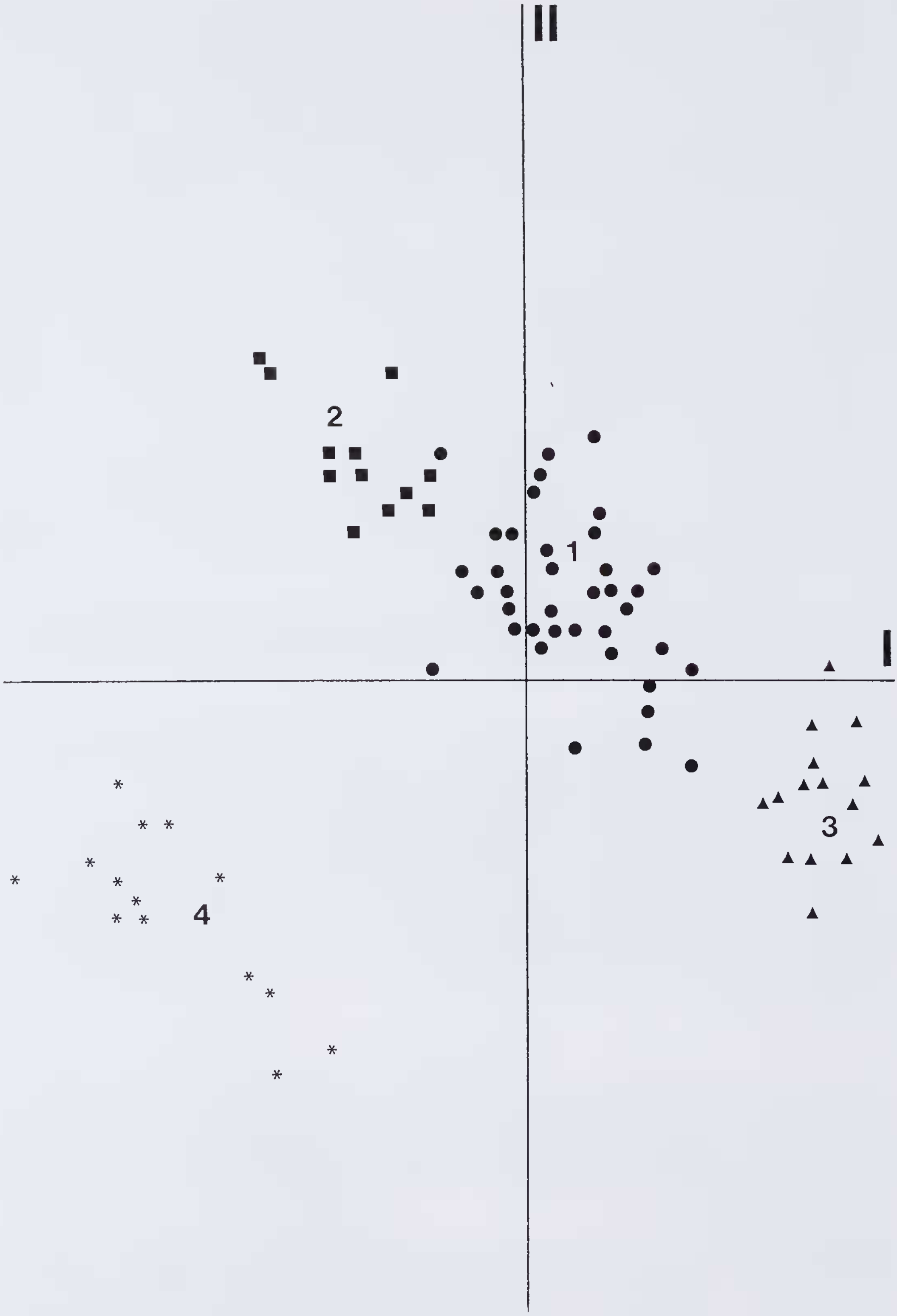

Fig. 11. Ordination of individual specimens using multi-dimensional scaling showing vector I against vector II. 1 (circles) = *T. xerophila* subsp. *xerophila*, 2 (squares) = *T. xerophila* subsp. *robusta*, 3 (triangles) = *T.* aff. *xerophila* (Baw Baws), 4 (asterisks) = *T. lanceolata*.

Table 3. Flavonoid/chalcone compounds

Taxon	Collection No.	Flavonoid/chalcone compounds 1	2	3	4	5	6	7	8	9	10
T. lanceolata	RER21	+	+	+	+	+					
	RER24	+	+	+	+	+					
	RER45	+	+	+	+	+					
	RER47	+	+	+	+	+					
	RER49	+	+	+	+	+					
	RER52	+	+	+	+	+					
	RER55	+	+	+	+	+					
	RER57	+	+	+	+	+					
	RER113	+	+	+	+	+					
	RER114	+	+	+	+	+					
T. xerophila subsp. *xerophila*	RER1	+					+	+	+		+
	RER4	+					+	+	+		+
	RER5	+					+	+	+		+
	RER7	+					+	+	+		+
	RER10	+					+	+	+		+
	RER31	+					+	+	+		+
	RER33	+					+	+	+		+
	RER36	+					+	+	+		+
	RER37	+					+	+	+		+
	NGW3289	+					+	+	+		+
T. xerophila subsp. *robusta*	RER19	+		+			+	+	+		+
	RER20	+					+	+	+		+
	RER26a	+					+	+	+		+
	RER27	+					+	+	+		+
	RER40	+					+	+	+		+
	RER44	+					+	+	+		+
T. vickeriana	RER92	+					+	+	+		+
	PYL1403	+					+	+	+		+
	PYL1404	+					+	+	+		+
	PYL1405	+					+	+	+		+
	PYL1407	+					+	+	+		+
	PYL1408	+					+	+	+		+
	PYL1410	+					+	+	+		+
	PYL1412	+					+	+	+		+

phila subsp. *xerophila.* The leaves of *T. vickeriana* are not only smaller but *c.* 90 µm thicker than leaves of *T. xerophila* subsp. *xerophila* and *c.* 200 µm thicker than leaves of *T. lanceolata.* The thick cuticle is also characteristic but could be phenotypic, with thicker cuticles related to growth at higher or colder localities. However, since *T. vickeriana* grows under *Eucalyptus pauciflora* with some of the same understorey species that occur with *T. xerophila* subsp. *xerophila* at Mt Buffalo (*e.g. Bossiaea foliosa*), and the altitudinal range at Mt Baw Baw and Mt Buffalo is similar, as is soil type (granite bedrock of Devonian age), rainfall and temperature, the differences may be genetically based.

Tasmannia xerophila subsp. *xerophila* and *T. xerophila* subsp. *robusta* differ only in leaf morphology and habit, and the two are indistinguishable on the bases of floral, fruit and leaf anatomical characters. *Tasmannia xerophila* subsp. *robusta* has leaves which are generally larger (7–14 cm cf. 3–9 cm long, and 20–30 mm cf. 7–17 mm wide) and often thinner, and is usually a more robust shrub (to small tree). The relatively sheltered conditions at Goonmirk Rocks (*T. xerophila* subsp. *robusta*) compared with the more open site at Frosty Hollow (*T. xerophila* subsp. *xerophila*) may allow the development of larger shrubs, although snow damage seems to result in most large specimens of *T. xerophila* subsp. *robusta* collapsing at the base. Alternatively, the area may be a local 'isolated' site and differences in plant form may be genetically based. Given that *T. xerophila* from the Errinundra Plateau is recognisably different, we have given it subspecific status.

Flavonoid compositions of all taxa support the findings of morphological analyses. A recent study of essential oils in Australian species of *Tasmannia* (Southwell & Brophy 1992) shows the distinctiveness of *T. lanceolata* from *T. xerophila* subsp. *xerophila*, but unfortunately the study did not include any plants of *T. vickeriana* or *T. xerophila* subsp. *robusta*. Flavonoid compositions of *T. xerophila* subsp. *xerophila* and *T. xerophila* subsp. *robusta* highlight the similarities between them. None of flavonoid data, morphological data or phenology supports a hybrid origin for *T. xerophila* subsp. *robusta*.

TAXONOMIC & NOMENCLATURE CONCLUSIONS

On the basis of this study, three distinct species of *Tasmannia* are recognised in Victoria: *T. lanceolata*, *T. xerophila* and *T. vickeriana*, the latter namc reinstated for *T.* aff. *xerophila* (Baw Baws). *Tasmannia* aff. *xerophila* (Errinundra Plateau) is here recognised as *T. xerophila* subsp. *robusta*.

Key to Victorian taxa of *Tasmannia*

1. Mature leaves usually less than 2 cm long, occasionally some to 2.5 cm long; mature berries burgundy (leaf apices obtuse, lamina coriaceous with veins obscure; stems finely tuberculate; tepals 2; forming aggregate fruit) .... **3. T. vickeriana**
1. Mature leaves 2 cm long or more (usually longer than 3 cm); mature berries black 2

2. Leaf apices acute, lamina thin, drying olive-green; stems smooth; tepals 3 or more; mature berries solitary, marked with a distinct furrow .... **1. T. lanceolata**
2. Leaf apices obtuse to subacute, lamina coriaceous, drying brownish rubescent; stems finely tuberculate; tepals 2; mature berries forming an aggregate fruit .... **2. T. xerophila**

1. Tasmannia lanceolata (Poir.) A.C.Smith, *Taxon* 18: 287 (1969).

Basionym: *Winterana* (as '*Winterania*') *lanceolata* Poir., *Encycl.* 8: 799 (1808). Type[1]: '*Labillardière s.n.* in herb. Desfontaines (*non vidi*), isotype (*ex* herb. Poiret) (P)' (see Vink 1970, p. 305).

Homotypic synonym: *Drimys lanceolata* (Poir.) Baill., *Hist. Pl.* 1: 159 (1868).

Heterotypic synonyms: *Tasmannia aromatica* R.Br. *ex* DC., *Syst.* 1: 445 (1817). *Drimys aromatica* (R.Br. *ex* DC.) F. Mueller, *Pl. Indig. Col. Vict.* 1: 20 (1860). Lectotype: Van Diemens Land [Tasmania], *R. Brown s.n.* in herb. DC. (G).

Drimys xerophila ['*aromatica*'] var. *β aromatica* P. Parm., *Bull. Sc. Fr. & Belg.* 27: 226, 300 (1896). Type: Mt Bischoff, Tasmania, *collector unknown* (P).

Bushy shrub often pyramidal in shape 1.5–4 m high, dioecious, single stemmed (sometimes up to 5-stemmed), stems smooth, reddish when young, older stems brownish red. *Leaves* alternate, blades lanceolate, 4–12 cm long, 8–35 mm wide, apex acute to subacute, grass green above, pale green and glaucous below; margins of blade flat, petiole 3–6 mm long; midrib and veins prominent. *Flowers* 3–6 per inflorescence; 1 flower per bract, with the outer bracts increasing in length and width acropetally; pedicels to 20 mm long. *Male flowers* with stamens up to

1. All typification based on annotated herbarium sheets (and in accordance with Willis 1957, pp. 188–9 and Vink 1970, p. 307). Types given in Parmentier (1896) are confused and some have been omitted.

Fig. 12. Habit drawings ×0.65, some with fruit. a — *T. lanceolata,* drawn from *R.E. Raleigh 109* (MELU). b — *T. xerophila* subsp. *xerophila,* enlargement (×4) shows tuberculate stem surface; drawn from *R.E. Raleigh 16* (MELU). c — *T. xerophila* subsp. *robusta,* drawn from holotype (MEL). d — *T. vickeriana,* drawn from *R.E. Raleigh 91* (MELU).

21, sterile carpels 1 (rarely 0 or 2). *Female flowers* 5–12 mm diameter; tepals 3–5 (rarely to 9) inserted laterally to the medial line 6.0–10 mm long, 1.5–2 mm wide; stamens absent; carpels 1 (rarely 2 fused) with 10–18 ovules, grooved. *Fruits* 1 (rarely 2) per pedicel, globose and deeply furrowed, 5.5–7.0 mm in diameter, deep maroon to glossy black when mature; pedicels to 25 mm long; seeds 4–13 per berry, black. (Fig. 12a)

Specimens Collected During Study

Victoria — Bonang Hwy, Martins Ck, alt. 320 m, *R.E.Raleigh 11*; Delegate River, Gunmark Rd, *R.E.Raleigh 13, 97*; Goonmirk Rocks, Errinundra NP, alt. 1100–1200 m, *R.E.Raleigh 21–24, 108, 109*; Frosty Hollow, Errinundra NP, alt. 970–1000 m, *R.E.Raleigh 28*; Mt Ellery, Errinundra NP, alt. 1291 m, *R.E.Raleigh 45–49*; Major Mitchell Plateau, Grampians NP, alt. 1080 m), *R.E.Raleigh 50, 52–59*; Beauty Spot, Otways, *R.E. Raleigh 113, 114*; Pirianda Gardens, Dandenong Ra., *R.E.Raleigh 115*.

New South Wales — Brindebella Ra., alt. 1646 m, *M.Duretto 111–120.*

2. Tasmannia xerophila (P.Parm.[2]) M.Gray, *Contr. Herb. Austral.* no. 26: 8 (1976).

Basionym: *Drimys xerophila* P.Parm., *Bull. Sci. France Belgique* 27: 225–6, 299–300 (1896). Type: Australian Alps, Victoria/New South Wales, *F. Mueller s.n.* (P).

Bushy spreading shrub to small tree, 0.6–4 m tall, dioecious; usually with clumped growth habit the result of root suckering, stems finely tuberculate, reddish when young, older stems ochre to reddish brown. *Leaves* alternate, becoming pseudo-whorled below the resting buds; blades oblanceolate to narrowly oblanceolate, (2–)3–14 cm long, 5–30 cm wide, coriaceous to rigid, apex obtuse to subacute; dark green above, pale green glaucous below; midrib prominent to obscured and finely tuberculate; margins of blade flat to slightly recurved; petiole 2–6 cm long. *Flowers* 1–16 per inflorescence; one flower per bract, with the outer of these bracts decreasing in length and width acropetally and caducous before new leaves have matured. *Pedicels* 7–12 mm long (male flowers), 7–15 mm long (female flowers). *Male flowers* with stamens 9–30, sterile carpels 1, rarely 2. *Female flowers* 4–8 mm diameter (excluding tepals); prophylls situated in the median plane orbicular to ovate, 3–6 mm long, tepals mostly 2, very rarely 3 or 4, inserted alternate to the prophylls, 5–7 mm long, 1–2 mm wide; stamenoids absent, carpels 1–8 (rarely to 11), with 2–9 ovules. *Fruits* 2–6 (rarely to 11) per pedicel, globose to short ovoid, 6.5–11 mm long, 5–10 mm broad, glossy black to glaucous at maturity, flesh near skin dark purple, white towards centre; pedicels 5.5–14 mm long; seeds 2–7 per berry, 2.5–3.5 mm long, 2–2.5 mm broad, black; aborted ovules pink.

Key to the subspecies

1. Shrub to 2.5 m tall; leaves (2–)3–9 cm long, 5–17 mm wide .... **2a.** subsp. **xerophila**
1. Shrub to small tree, 2.5–4 m tall; leaves 7–14 cm long, 20–30 mm wide; Goonmirk Rocks and Mt Ellery only .... **2b.** subsp. **robusta**

2. Parmentier (1896) treats *Drimys aromatica* in part as synonymous with *D. xerophila* but does not include the type of *D. aromatica* in *D. xerophila*, nor does he list *D. aromatica* as a synonym of *D. xerophila*. He does, however, list *D. xerophila* ['*aromatica*'] var. *β aromatica* (with a different type to *D. aromatica*) as a synonym of *D. xerophila*. This variety is referable to *D. lanceolata* and what Parmentier labelled (in herbarium) as typical *D. aromatica* is referable to *D. xerophila* (Willis 1957). In spite of this confusion (and the fact that in the sense of Parmentier *D. aromatica* is synonymous with *D. xerophila*), *D. xerophila* does not 'definitely include the holotype' (see ICBN, Art. 63.1 & 63.2) of *D. aromatica* and is therefore legitimate.

2a. Tasmania xerophila subsp. **xerophila**

HETEROTYPIC (INFORMAL) SYNONYM: *Drimys piperita* Hook. f. 'entity 39. *xerophila*' Vickery, *Blumea* 18: 349 (1970).

MISAPPLIED NAME: *Drimys aromatica sensu* P.Parm. *Bull. Sci. France Belgique* 27: 298 (1896), *non* (R.Br. *ex* DC.) F.Muell. SPECIMEN EXAMINED: Australian Alps, Victoria/New South Wales, *C.Walter s.n.* (P) (see Willis 1957, p. 189).

Small shrub to 2.5 m high. *Leaves* (2–)3–9 cm long, 7–17 mm wide. *Flowers* 1–16 per inflorescence. *Female flowers* with carpels 2–6 (rarely to 11) and ovules 2–9 per carpel. (Fig. 12b)

SPECIMENS COLLECTED DURING STUDY

Victoria — Mt Buffalo NP, alt. 1400 m, *R.E.Raleigh 1–10, 78–80, 86*; Delegate R., Gunmark Rd, *R.E.Raleigh 12, 14–16, 96*; Frosty Hollow, Errinundra NP, alt. 970–1000 m, *R.E.Raleigh 29–38, 98–102*; Falls Creek, alt 1700 m, *N.G.Walsh 3288, 3289*; Chinamans Flat beside Hutchinsons Creek, alt. 880 m), *K.E.Wilson 320.*

New South Wales — Mt Selwyn, alt. 1300 m, *R.E.Raleigh 72–77*; 1 km SW Tumut Pond, alt. 1300 m), *R.E.Raleigh 81–84*; Beside road, 10 km from Cabramurra, *R.E.Raleigh 85*; Thredbo R. near Thredbo village, Mt Kosciusko, alt. 1250 m), *P.Y.Ladiges 1422–1425*; Dead Horse Gap, Mt Kosciusko, alt. 1500 m), *P.Y.Ladiges 1426–1428*; Alpine Way, 2 km WSW Dead Horse Gap, Mt Kosciusko, alt. 1500 m), *P.Y.Ladiges 1429–1431.*

2b. Tasmannia xerophila subsp. **robusta** Raleigh *subsp. nov.*

A varietate typica habitu altiore (2.5–4 m), foliis longioribus (7–14 cm) et latioribus (20–30 mm) differt.

TYPUS: Goonmirk Rocks, East Gippsland, Victoria, 8 Jan. 1992, *R.Raleigh 103.* HOLOTYPUS: MEL 2014065 (female plant); ISOTYPUS: MELU (female plant).

Shrub to small tree, 2.5–4 m tall. Leaves 7–14 cm long, 20–30 mm wide, with petioles 3.5–6 mm long. *Flowers* 5–8 per inflorescence. *Female flowers* with carpels 1–8, ovules 3–7 per carpel. (Fig. 12c)

SPECIMENS COLLECTED DURING STUDY

Victoria — Goonmirk Rocks, Errinundra NP, alt. 1100–1200 m), *R.E.Raleigh 18–20, 25, 26, 26a, 27, 27a, 103–107*; Mt Ellery, Errinundra NP, alt. 1291 m, *R.E.Raleigh 39–44.*

3. Tasmannia vickeriana (A.C.Smith) A.C.Smith, *Taxon* 18: 287 (1969).

BASIONYM: *Drimys vickeriana* A.C.Smith, *J. Arnold Arb.* 24: 130 (1943). TYPE: Mt Mueller, Victoria, *Luehmann & French s.n.* (A).

HETEROTYPIC SYNONYMS: *Drimys xerophila* ['*aromatica*'] var. *alpina* F.Muell. *ex* P.Parm., *Bull. Sci. France Belgique* 27: 226, 300 (1896). TYPE: Baw Baw Ranges, Victoria, *F. Mueller s.n.* (P).

Drimys lanceolata var. *parvifolia* Vickery, *Proc. Linn. Soc. New South Wales* 62: 83 (1937). TYPE: Upper Yarra, Victoria, *Staer s.n.* (NSW).

Plants as for *T. xerophila*, but 0.5–1.2 m in height. *Leaves* compact, 0.8–2(–2.5) cm long, 2–6 mm broad, apex obtuse, veins obscured, petiole 1.5–3.5 mm long. *Flowers* 1–15 per inflorescence, pedicels 3–10 mm long. *Male flowers* with stamens 8–26, sterile carpels 1 (rarely 2). *Female flowers* with stamens absent, carpels 1–6, with 3–6 ovules. *Fruit* 1–3 (rarely 4) per pedicel, globose to short ovoid, 6–12 mm long, 6–10 mm broad, burgundy at maturity, flesh near skin pale burgundy, white towards centre; pedicels 4–11 mm long; seeds 2–5 per berry, 2–3 mm long, 1.5–2 mm broad, black; aborted ovules white. (Fig. 12d)

SPECIMENS COLLECTED DURING STUDY

Victoria — Mt Baw Baw: Edge of car park near Mt Baw Baw ski village, alt. 1563 m, *R.E.Raleigh 90*; 1 km below Mt Baw Baw ski village, alt. 1500 m, *R.E.Raleigh 91–95*; Mt Baw Baw ski village, alt. 1563 m, *R.E.Raleigh 112*; Mt Baw Baw ski village, alt. 1563 m, *P.Y.Ladiges 1403–1412.*

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